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Collembola of Cold Pyrenean habitats

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Abstract

This study contributes data about species composition, diversity and structure of the Collembolan communities in habitats exposed to the temporary cold of the snowy period in mountains (TCH), by comparing with habitats exposed to permanent cold all along the year (PCH). 138 samples have been collected in the Central Pyrenean range following the thaw line according to an altitude gradient from 1 500 m to 2 800 m.

Species richness and diversity were larger in TCH than in PCH probably because of the great variety of habitats and the time of sampling. In TCH, cryophilous species were not very numerous, abundant or frequent and the communities were dominated by non-cryophilous generalistic species like *Pseudisotoma monochaeta*, *Folsomia quadrioculata*, *Isotomiella minor*, and *Anurophorus oredonensis*. Most of the Collembola fauna of TCH consist of species that are also active there during the warm season. In contrast, PCH contain numerous cryophilous species that are both abundant and frequent.

Factorial correspondence analysis reveals that this community is loosely structured although the first factor is interpreted as a gradient of increasing cold and provides an objective discrimination between TCH and PCH fauna and samples.

Keywords: Collembola, soil, cold habitats, thaw, species richness, mountain fauna.

Collemboles des milieux froids des Pyrénées centrales

Résumé

Ce travail fournit des données sur la composition spécifique, la diversité et la structure des peuplements collembologiques des milieux soumis au froid temporaire de la période enneigée en montagne (TCH), en comparaison avec ceux des milieux soumis au froid permanent pendant toute l'année (PCH). 138 relevés ont été réalisés dans les Pyrénées centrales en suivant le front de déneigement selon un gradient altitudinal de 1 500 m à 2 800 m.

La richesse et la diversité spécifiques sont plus importantes dans les TCH que dans les PCH ce qui semble en rapport avec la variété des biotopes prélevés et le moment particulier des prélèvements. Dans les TCH, les espèces cryophiles sont peu nombreuses, peu abondantes et rares et le peuplement est dominé par des espèces eurybiontes non cryophiles telles que *Pseudisotoma monochaeta*, *Folsomia quadrioculata*, *Isotomiella minor* et *Anurophorus oredonensis*. Le peuplement est plus proche de celui mis en évidence, dans les mêmes habitats pendant la période déneigée que de celui des PCH. L'essentiel du peuplement des TCH est donc composé d'espèces présentes aussi pendant la belle saison et qui résistent au froid de l'hiver. Par contre les PCH contiennent de nombreuses espèces cryophiles fréquentes et abondantes.

L'analyse des correspondances montre que le peuplement est peu structuré bien que le premier facteur puisse être interprété comme l'axe de la permanence croissante du froid et discrimine assez bien la faune et les relevés des TCH de ceux des PCH.

Mots-clés : Collemboles, sol, milieux froids, déneigement, richesse spécifique, faune de montagne.

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INTRODUCTION

Collembola constitute a major group of animals in cold edaphic habitats both by its diversity and its adaptation. The studies performed to date have brought a wealth of systematic and ecophysiological data on Antarctic, Arctic, Scandinavian and Canadian fauna (review in Aitchinson 1984; in Joose,1983; in Sømme & Block 1991; in Vernon & Vannier, 1990; in Leather *et al.* 1994) but results on the ecology of communities are scarce.

For the mountain fauna of southern Europe, some biological and systematic studies have been undertaken in the Alps (Gisin, 1943; Handschin, 1919 and 1924; Schenker, 1983; Sømme, 1979; Zettel, 1984) but without any ecological analysis. On the other hand, a broad study of the ecology of Collembola in the central Pyrenees range was made by Cassagnau (1961) and the data processed by Salem (1973) using correspondence analysis. These studies report the existence of eighteen Collembola assemblages and, for the first time, a lot of information on the cryophilous fauna. By far the most extensive study of community ecology in the permanently cold environment of mountains has been conducted by Deharveng (1975) in the Pyrenees, stressing the existence of abundant and diversified cryophilous fauna of particularly ancient lineages. It should be noted that the Pyrenees are rather suitable for cold environment studies because the last glaciations and post-glacial warming did not reach the whole mountain range (Jeannel,1947) allowing the persistence of an ancient cold fauna that would otherwise have disappeared from northern Europe under the effect of the glaciations.

However, the studies by Cassagnau (1961) and Deharveng (1975) especially concern fauna exposed to permanent cold (temperature range −2°C-+6°C) all along the year, *i.e.* linked to permanent neves, frozen ground, sources and cold springs between 2 300 m and 3 000 m of altitude (Permanently Cold Habitats: PCH). These works stress the existence of a rich cryophilous fauna. On the other hand, no extensive studies have been undertaken in areas with regular snow cover in winter (Temporarily Cold Habitats: TCH). In these TCH habitats, and despite the buffering effect of the snow cover, temperatures oscillate between −2°C and +2°C and the ground is generally frozen in winter.

The aims of the present study are:

– to characterize the TCH Collembola community in terms of species composition, diversity, abundance, frequency distribution and structure;

– to assess the relative importance of cryophilous and non-cryophilous species;

– to assess the affinity between TCH and PCH communities.

MATERIAL AND METHODS

Study area

Samples were collected in the high valley of the Aure and in the Neouvieille range in the Pyrenees mountains. The Neouvielle range forms an imposing north-south barrier in the Central Pyrenees, 150 kilometers from the Atlantic ocean and 230 kilometers from the Mediterranean sea. Altitudes range from 1 500 to 2 800 meters, from the mountain belt to the top of the alpine belt following the right bank of the Aure river, around the lakes of Oredon and Aumar and along the valley of the Estaragne until the upper cirque of Estaragne.

Sampling

A total of 136 samples were collected. They consisted essentially of samples of litter, humus, superficial ground, grassland and mosses. Northern orientation was always chosen or local situations favouring low temperatures: between −2°C and 6°C under and around the snow, most of the ground being frozen.

The TCH fauna of mountains are difficult to sample in winter because the snow cover is thick. This fauna appears at the beginning of the thaw. We collected 121 samples by following the thaw line, according to altitude progression. Sampling started in March at an altitude of 1 500 meters (level of the montane ~~mountain~~ belt) and ended at 2 500 meters in August (level of the alpine belt). Fifteen samples of PCH were also collected in September between 2 400 and 2 800 meters of altitude at the level of the base of the permanent neves in the alpine belt and high alpine belt. To summarize, sampling was distributed among the following levels:

TCH:

– montane ~~mountain~~ belt: fir forest, beech forest or beech-fir forest;

– subalpine belt: pine forest, clear pine rhododendron forest, rhododendron heath, lawn;

– alpine belt: lawn, screes.

PCH:

– high alpine belt: vicinity of sources and cold springs, rocks, screes, neves.

For each sample we took an indicative volume of 500 cm^3 of substrate from the top 5 cm of soil. Four parameters were recorded: temperature, altitude, vegetation-cover and state of ground (frozen or non-frozen).

Collembola fauna was extracted over 7 to 10 days at the Toulouse laboratory, using a Berlese apparatus. Collembola were collected in ethanol, cleared in lactic acid and mounted in gum Arabic for identification.

Identification of Species

A total of 98 species were found (*tables* 1 and 2). However, *Pseudisotoma monochaeta*, characterized by specific criteria (Cassagnau, 1961; Deharveng, 1975), presents five chromatic varieties. As the taxonomic and ecological status of these chromatic forms have not yet been clarified we differentiated them for this work by associating the name of the species to their colour: e.g. gray *Pseudisotoma monochaeta*, mauve *Pseudisotoma monochaeta* etc.

Ecological status of species

The status of the cryophilous species in the Pyrenees has already been defined (Cassagnau, 1961; Deharveng, 1975). Three types of species accomplish their biological cycle at low temperatures:

- those requiring constantly low temperatures (0°C to 6°C), linked to alpine and high alpine belts around sources of cold such as persistent neves, northern springs and melt water;
- those populating for historic reasons and/or thermal preferences, caverns and high mountain habitats;
- those rather met in the snow-covered season and often linked to snow cover and disappearing during the snow-free season.

Data analysis

Data were submitted to various types of quantitative analysis.

1. Percentages and their graphic representations describe the cryophilous status, abundance, and frequency of species.
2. Species richness of the samples was evaluated by the Monod estimator (Lauga & Joachim, 1987)
3. Diversity analysis was conducted using standard diversity descriptors: Berger-Parker Index, evenness, β diversity (Whittaker, 1960).
4. Multivariate analysis: factorial correspondence analysis was used (SAS, 1989).

RESULTS - DISCUSSION

Global species richness, Abundance and Frequency

1 - Temporarily cold habitats (TCH)

Species richness

The species richness was high. 92 species were found (*table* 1), totaling 23 698 individuals in the 121 samples corresponding to 90.3% of the total species richness (N = 101.9) provided by the Monod estimator. The plot of the cumulative number of species versus the sampling effort (*fig.* 1 a) seems to show that even if the total richness is not exactly reached, few additional taxa are expected.

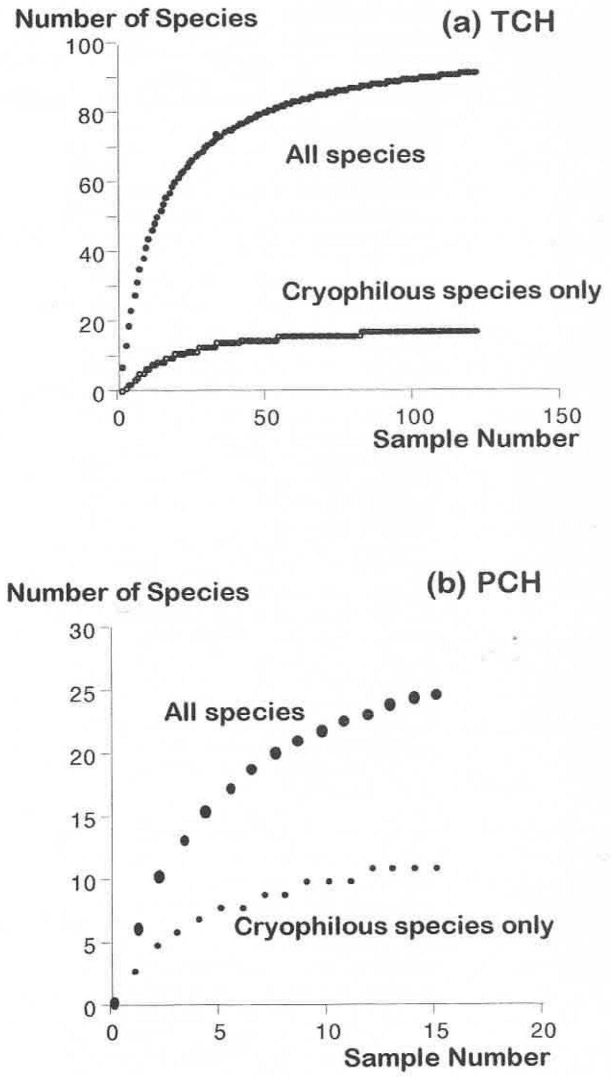


Figure 1. – Plot of the cumulative number of species versus sample number for all species and cryophilous species only in (a) TCH and (b) PCH.

Abundance and Frequency

The graph of the species abundance versus their rank (*fig.* 2) reveals that just five species gather more than 50% of all the individuals: gray *Pseudisotoma monochaeta*, *Xenylla biroi*, *Anurophorus oredonensis*, *Folsomia quadrioculata*, mallow *Pseudisotoma monochaeta*. *Xenylla biroi* seems to be a particular case because of an exceptional proliferation in one sample (3 052 individuals). The four other species are generalistic with a high reproduction rate, often being

Table 1. – List of TCH Species. Abbrev.: Abbreviation; Abun.: Abundance; Cry.: Cryophilous species (c); # Sam.: Number of samples.

Species	Abbrev.	Cry	Abund	# Sam
Anurophorus oredonensis Cassagnau 1953	AnuOre		2615	30
Arrhopalites spe	ArrSpe		1	1
Bourletiella radula Gisin 1946	BouRad		15	2
Bilobella aurantiaca Caroli 1910	BilAur		12	2
Brachystomella parvula Schaeffer 1896	BraPar		1004	34
Ceratophysella armata (Nicolet) 1841	CerArm		2	2
Ceratophysella bidentata Cassagnau 1954	CerBid	c	119	11
Ceratophysella cylindrica Cassagnau 1959	CerCyl	c	5	1
Ceratophysella denticulata	CerDen		147	22
Ceratophysella duodecimoculata Steiner 1955	CerDuo	c	8	4
Ceratophysella elegans Cassagnau 1959	CerEle	c	53	4
Coloburella zangherii (Denis) 1924	ColZan		400	6
Desoria propinqua (Axelson) 1902	DesPro		23	4
Deutonura deficiens ▯eharveng 1979	DeuDef		1	1
Deutonura monticola Cassagnau 1954	DeuMon		25	14
Dicyrtomina minuta (O.Fabricius) 1783	DicMin		275	7
Dicyrtoma ornata Nicolet 1842	DicOrn		11	4
Entomobrya nivalis (Linné) 1758	EntNiv		368	38
Entomobrya quiquelineata Börner 1901	EntQui		1	1
Folsomia decopsis Steiner 1958	FolDec		2	1
Folsomia manolachei Bagnall 1939	FolMan		50	11
Folsomia nigromaculata Najt 1980	FolNig	c	122	6
Folsomia quadrioculata Tullberg 1980	FolQua		1934	63
Folsomia sensibilis Kseneman 1936	FolSen		174	37
Friesea albida Stach 1949	FriAlb		42	9
Friesea albida pyrenaïca Cassagnau 1958	FriAPy		10	5
Friesea albida atypica Cassagnau 1958	FriAty		15	6
Friesea mirabilis Tullberg 1871	FriMir		344	13
Friesea truncata Cassagnau 1958	FriTru		36	6
Gnathisotoma bicolor Cassagnau 1958	GnaBic	c	11	6
Heteromurus major Moniez 1889	HetMaj		336	27
Hypogastrura boldorii Schaeffer 1900	HypBol		20	1
Hypogastrura elevata Cassagnau 1959	HypEle		222	9
Isotoma fennica Reuter 1895	IsoFen		10	1
Isotomiella minor (Schaeffer) 1896	IsoMin		529	44
Isotoma notabilis Schaeffer 1896	IsoNot		208	22
Isotoma viridis Bourlet 1839	IsoVir		66	8
Isotomurus palustris (Müller) 1776	IsoPal		3	2
Isotomurus cassagnaui Deharveng-Lek 1993	IsoCas		217	1
Isotomurus maculatus (Börner) 1901	IsoMac		10	1
Isotomurus spe	IsoSpe	c	132	14
Lepidocyrtus curvicollis Bourlet 1839	LepCur		217	16
Lepidocyrtus cyaneus (Tullberg) 1872	LepCya		271	34
Lepidocyrtus lanuginosus Gmelin 1788	LepLan		47	6
Lepidocyrtus spe	LepSpe		169	5
Megalothorax minimus Willem 1900	MegMin		1	1
Mesaphorura krausbaueri Börner 1901	MesKra		382	23
Metaphorura affinis Agren 1903	MetAff		12	3
Mucrella acuminata Cassagnau 1958	MucAcu		14	3
Neanura muscorum (Templeton) 1835	NeaMus		12	9
Odontellina nivalis Cassagnau 1959	OdoNiv	c	147	3
Oligaphorura absoloni (Börner) 1901	OliAbs		55	3
Oncopodura crassicornis Shoebotham 1911	OncCra		19	3
Orchesella orientalis Stach 1960	OrcOri		2	1
Orchesella spe	OrcSpe		2	2
Orogastrura dilatata Cassagnau 1960	OroDil	c	54	12
Orogastrura pallida Cassagnua 1954	OroPal	c	47	2
Proisotoma palustris Cassagnau 1959	ProPal	c	413	5
Protaphorura armata (Tullberg) 1859	ProArm		572	54
Protachorutes pyreneus Cassagnau 1953	ProPyr		107	23
Pseudachorudina bougisi Delamare 1951	PseBou		37	6
Pseudachorutes parvulus Denis 1934	PsePar		7	4
Pseudanurophorus binoculatus Kseneman 1934	PseBin	c	178	12
Pseudisotoma monochaeta (Kos) 1942 (beige)	PseMbe		284	19
Pseudisotoma monochaeta (Kos) 1942 (white)	PseMoB	c	181	11
Pseudisotoma monochaeta (Kos) 1942 (gray)	PseMoG		3397	72
Pseudisotoma monochaeta (Kos) 1942 (mauve)	PseMoM		1182	40
Pseudisotoma monochaeta (Kos) 1942 (black)	PseMoN	c	18	7
Pseudisotoma monochaeta rose (Kos) 1942	PseMoR		32	1
Pseudosinella alba (Packard) 1873	PseAlb		27	6
Pseudosinella suboculata Bonet 1931	PseSub		135	20
Rusekella peyrei (Cassagnau) 1955	RusPey		34	6

Table 1. – Continued.

Species	Abbrev.	Cry	Abund	# Sam
Schaefferia emucronata Absolon 1900	SchEmu	c	16	4
Sminthurides alpinus Cassagnau 1960	SmiAlp	c	33	8
Sminthurides malmgreni	SmiMal	c	307	5
Sminthurinus aureus (Lubbock) 1862	SmiAur		26	1
Sminthurinus Spe	SmiSpe		20	5
Sminthurinus niger (Lubbock) 1876	SmiNig		157	4
Sminthurinus signatus (Krausbauer) 1898	SmiSig		9	2
Sphaeridia pumilis (Krausbauer) 1898	SphPum		754	7
Superodontella nana Cassagnau 1954	SupNan		685	13
Tetracanthella orbacetensis Cassagnau 1959	TetOrb		15	1
Tetracanthella pseudomontana Cassagnau 1953	TetPse		20	4
Tetracanthella pyrenaïca Cassagnau 1953	TetPyr		437	36
Tetracanthella uniseta Deharveng 1987	TetUni		21	3
Tomocerus minor (Lubbock) 1862	TomMin		33	14
Triacanthella perfecta Denis 1926	TriPer		190	19
Tullbergia callipygos (Börner) 1903	TulCal		4	2
Vertagopus spe	VerSpe		8	2
Willemia anophtalma Boerner 1901	WilAno		261	9
Xenylla biroi Stach 1926	XenBir		3062	5
Xenylla brevicauda Tullberg 1869	XenBre		7	1

found in abundance in extreme habitats. Many species were not very abundant and were represented by only a few specimens. Among the cryophilous species, *Proisotoma palustris* and *Sminthurides malmgreni* colonizing humid cold habitats were the most abundant.

The graph of the species frequency versus their rank (*fig.* 3) reveals that three species were rather constant, they were found in more than 50% of the samples (gray *Pseudisotoma monochaeta*, *Folsomia quadrioculata* and *Protaphorura armata*). Nine secondary species were found in at least 25% of the samples and the other species were rare only being found in less than 25% of the samples. Except *Proisotoma palustris* and *Sminthurides malmgreni*, most cryophilous species were both accidental and rare.

Table 2. – List of PCH species. Abbr.: Abbreviation; Abun.: Abundance; Cry.: Cryophilous species; # Sam.: Number of samples.

Species	Abbrev.	Cry	Abund	# Sam
Anurophorus oredonensis Cassagnau 1953	AnuOre		181	8
Ceratophysella bidentata Cassagnau 1954	CerBid	c	122	2
Ceratophysella recta Cassagnau 1958	CerRec	c	293	10
Entomobrya nivalis (Linné) 1758	EntNiv		2	1
Folsomia quadrioculata Tullberg 1871	FolQua		1862	8
Gnathisotoma bicolor Cassagnau 1958	GnaBic	c	4	1
Hypogastrura elevata Cassagnau 1959	HypEle		6544	9
Hypogastrura estaranhensis Cassagnau 1958	HypEst	c	9	1
Isotomurus palustris (Müller) 1776	IsoPal		87	2
Isotomurus spe	IsoSpe	c	452	4
Orchesella spe	OrcSpe		5	2
Protaphorura armata (Tullberg) 1869	ProArm		1119	7
Proisotoma palustris Cassagnau 1959	ProPal	c	997	2
Pseudisotoma monochaeta (Kos) 1942 (white)	PseMoB	c	717	10
Pseudisotoma monochaeta (Kos) 1942 (gray)	PseMoG		6355	13
Pseudisotoma monochaeta (Kos) (mauve)	PseMoM		1724	2
Pseudisotoma monochaeta (Kos) 1942 (black)	PseMoN	c	1347	6
Psedosinella suboculata Bonet 1931	PseSub		38	7
Schaefferia emucronata Absolon 1900	SchEmu	c	132	6
Sminthurinus spe	SmiSpe		42	1
Tetracanthella elevata Cassagnau 1959	TetEle	c	39	2
Tetracanthella estaranehensis Cassagnau 1959	TetEst		26	3
Tetracanthella irregularis Deharveng 1987	TetIrr		6	1
Tetracanthella uniseta Deharveng 1987	TetUni		7	2
Triacanthella frigida Cassagnau 1959	TriFri	c	681	5

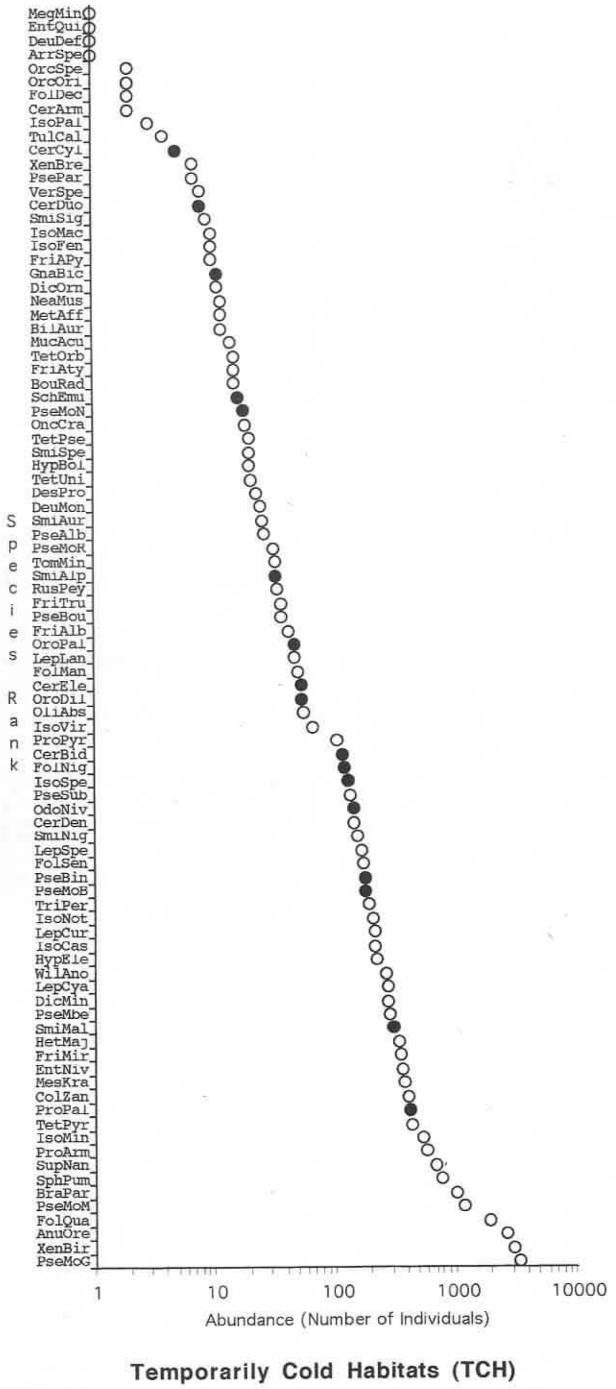


Figure 2. – Rank abundance graph in Temporarily Cold Habitats (TCH on log. scale). o: non cryophilous species, ●: cryophilous species.

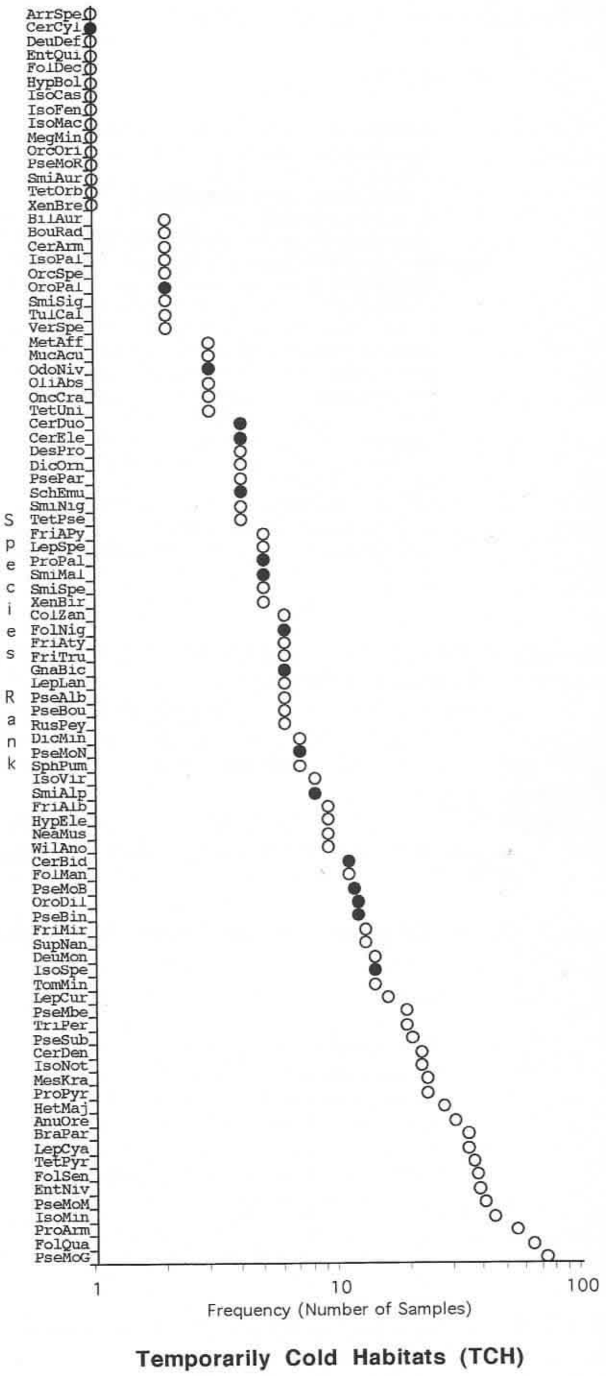


Figure 3. – Rank frequency graph in Temporarily Cold Habitats (TCH on log. scale). o: non cryophilous species, ●: cryophilous species.

The correlation coefficient between abundance and frequency for all species (*fig.* 7 a) is moderate but highly significant ($\rho = 0.763$, $p < 0.01$).

Taking into account both abundance and frequency, three species reported as "fundamental" (in more of 80% of samples) by Cassagnau (1961) were also abundant and frequent in this community: *Pseudisotoma monochaeta*, *Folsomia quadrioculata*, *Protaphorura armata*. They were rather generalistic species. The gray *Pseudisotoma monochaeta* dominated the Collembola community. Most species of this community have also been reported in the same kind of habitats during the snow-free season (Cassagnau, 1961).

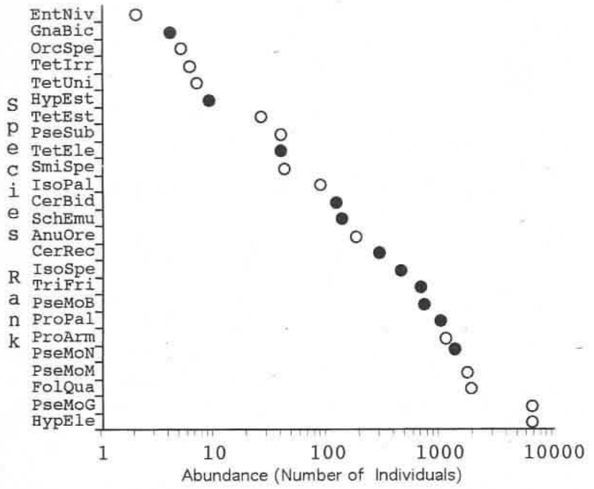
2 - Permanently cold habitats (PCH)

Species richness

The species richness was low. 25 species were found (*table* 2) totaling 22791 individuals in 15 samples corresponding to 83.3% of the total species richness (N = 30.01) given by the Monod estimator. The plot of the cumulative number of species versus the sampling effort (*fig.* 1 b) reveals that few species were lacking from our samples. However, the real species richness presents a light difference with the estimator because the number of samples was rather limited.

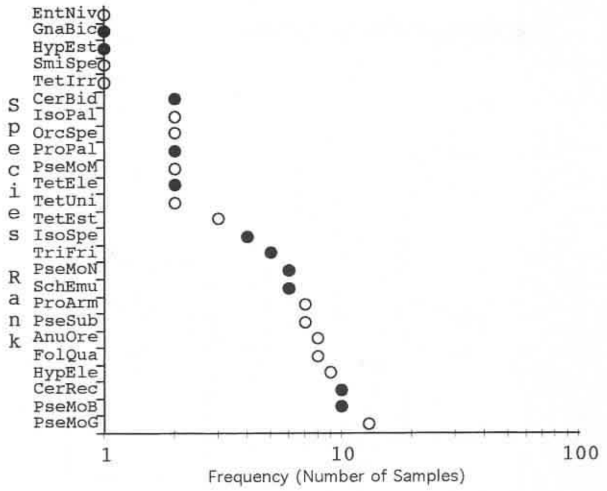
Abundance and Frequency

The graph of species abundance versus their rank (*fig.* 4) reveals that two species only gathered more than 50% of all the individuals: *Hypogastrura elevata* and gray *Pseudisotoma monochaeta* that are generalistic species, not specialized and with a high reproduction rate. It is noticeable that the set of cryophilous species in the present study was larger here in TCH. The graph of species frequency versus their rank (*fig.* 5) reveals that one species was fundamental (in more than 80% of the samples), gray *Pseudisotoma monochaeta*. Five species were constant (in more than 50% of the samples) including two cryophilous (white *Pseudisotoma monochaeta* and *Ceratophysella recta*) and six were secondary (in more than 25% of the samples) including four cryophilous (*Schaefferia emucronata*, black *Pseudisotoma monochaeta*, *Triacanthella frigida* and *Isotomurus* spe). The other species were accidental or rare. The cryophilous species were both more abundant and more frequent in PCH than in TCH.



Permanently Cold Habitats (PCH)

Figure 4. – Rank abundance graph in Permanently Cold Habitats (PCH on log. scale). o: non cryophilous species, ●: cryophilous species.



Permanently Cold Habitats (PCH)

Figure 5. – Rank frequency graph in Permanently Cold Habitats (PCH on log. scale). o: non cryophilous species, ●: cryophilous species.

The correlation coefficient between abundance and frequency for the all species (*fig.* 7 b) was moderately high and very significant ($r = 0.708$, $p < 0.01$). It is worth noting that the slope of regression line is steeper than that of TCH which means that, for a given abundance, the frequency tends to be higher in PCH than in TCH.

By comparing the abundance and the frequency, species that dominate the community are *Pseudisotoma monochaeta*, *Folsomia quadrioculata*, *Hypogastrura elevata*: all generalistic species.

Diversity

The Berger-Parker Index (*fig.* 6 a) was slightly higher in TCH than in PCH but the difference was not significant (Mann-Withney, $U = 1048$, $p = 0.176$ NS) (*fig.* 6 a).

On the other hand, evenness was greater in PCH than in TCH (*fig.* 6 b), and here the difference is significant (Mann-Withney, $U = 574$, $p = 0.036$). The greater evenness in PCH is partly explained by the fact that at the time of sampling (end of summer), populations were in equilibrium because they were little or not at all affected by reproduction. However, sampling of TCH was done at the beginning of the thaw (these habitats being unreachable before). At this time many species were in the inactive egg stage or at the beginning of their reproduction. These inequalities were further emphasized because of high reproduction rates in many species. Thus, many samples were dominated by numerous young individuals of some species and they generally revealed larger irregularities in the number of individuals from one to another depending upon the reproductive rates and the time of reproduction.

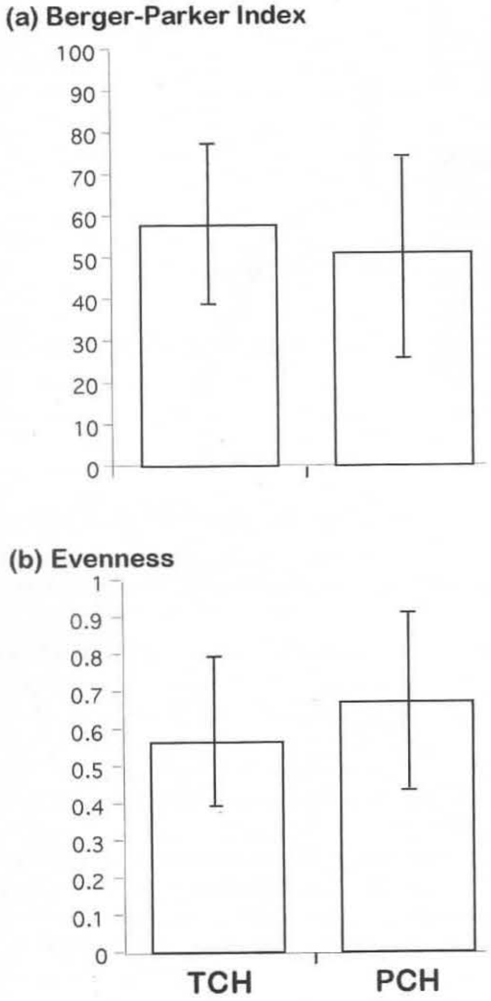


Figure 6. – Mean values (+ – SEM) of (a) Berger-Parker Index and (b) Evenness in TCH and PCH samples.

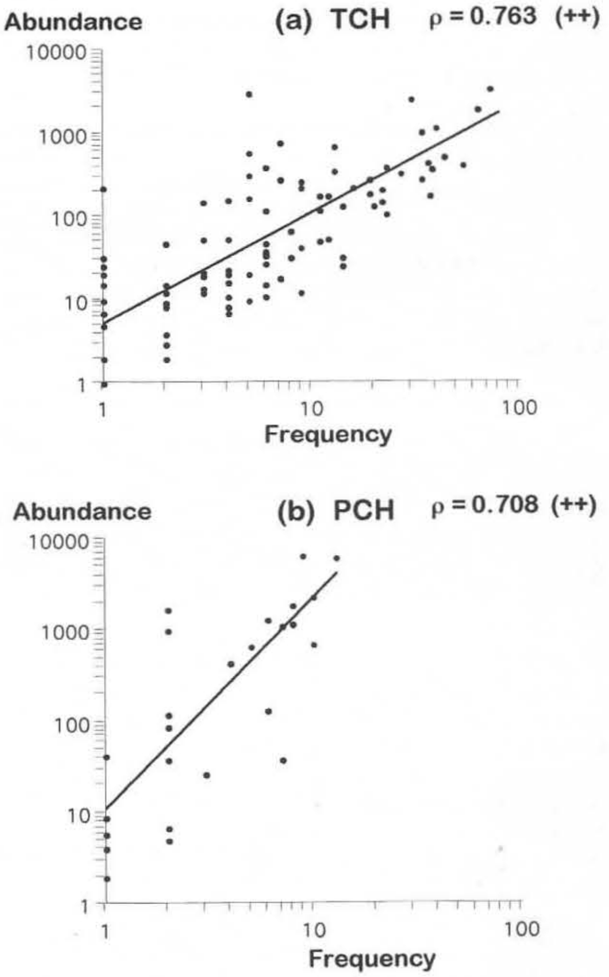


Figure 7. – Linear relationship between abundance and frequency (both on log scale) in (a) TCH (a) and (b) PCH. ρ values are Spearman's rank correlation, both highly significant (++, $p < 0.01$).

The high β diversity (Whittaker, 1960) of TCH (mean = 9.43) can be explained by the great heterogeneity (degree of water saturation of the soil, plant formation, depth of snow cover, microclimate and altitude levels). The β diversity was low in PCH (mean = 2.15) because samples were more homogeneous than in TCH. PCH present a greater homogeneity at least with respect to altitude and microclimate.

Significant differences between the index of evenness and β diversity show that PCH presented a greater homogeneity than TCH within each sample and between all samples.

Cryophilous versus non-cryophilous species, influence of altitude

Among the 92 species found in TCH, only 17 (*table* 1, *figs*. 1 a, 2 and 3) were cryophilous (18.5%) with 7.8% of individuals in 53% of samples. The Monod estimator of cryophilous species richness gave a value of 19.6 (19.3% of the estimated global richness). Cryophilous species were thus neither numerous, nor abundant but they were spread through more than half of the samples.

Gnathisotoma bicolor, *Orogastrura pallida*, *Pseudanurophorus binoculatus* and *Schaefferia emucronata* were found up to 200 meters below their lower altitude limit, reported during the warm season, because of thermal conditions (northern orientation for example).

Among the 25 species found in PCH, 11 (*table* 2, *figs*. 1 b, 4 and 5) were cryophilous (44%) including 21% of the individuals in 100% of the samples. The Monod estimator of cryophilous species richness led a value of 13.34 (44.45% of the estimated global richness).

Ten cryophilous species were found in TCH: *Ceratophysella cylindrica*, *Ceratophysella duodecimoculata*, *Ceratophysella elegans*, *Folsomia nigromaculata*, *Odontellina nivalis*, *Orogastrura dilatata*, *Orogastrura pallida*, *Pseudanurophorus binoculatus*, *Sminthurides alpinus* and *Sminthurinus malmgreni*. They were associated with snow, cold water or with particular orientations. They never reached PCH, perhaps because of the altitude and the lack of rich organic soil.

Seven cryophilous species were found in both TCH and PCH: *Ceratophysella bidentata*, *Gnathisotoma bicolor*, *Isotomurus* sp. (the species *transversalis* is to be described, Cassagnau personal communication), *Proisotoma palustris*, white *Pseudisotoma monochaeta*, black *Pseudisotoma monochaeta*, *Schaefferia emucronata*.

Four cryophilous species were found in PCH only: *Ceratophysella recta*, *Hypogastrura estaranhensis*, *Tetracantella elevata* and *Triacanthella frigida*. They have already been reported by Deharveng (1975) and Cassagnau (1961). These are cryophilous specialist species combining the requirements of high altitude and low temperatures and that never descend short of their altitude limits even if the snow cover is permanent.

In TCH, we did not find any of the cryophilous species reported by Cassagnau (1961) in the snowy season: *Hypogastrura manubrialis neglecta*, *Ceratophysella pyrenaïca*. Similarly in PCH *Hypogastrura chouardi*, *Friesea inermis*, *Folsomia sexoculata*, *Pseudachorudina angelieri* were never found. However, all these species are known to be rare or accidental. Thus, it is not surprising that they were lacking in our samples.

Important differences were found between PCH and TCH concerning the nature, the abundance and the frequency of the cryophilous species: in TCH, cryophilous species were scarce and their individuals were not abundant, while in PCH, cryophilous species were numerous and their individuals abundant.

PCH always being higher in altitude than TCH, the influence of this parameter on community composition and structure can be questioned. We have grouped into three sets the TCH samples corresponding to large variations in altitude and plant formation to evaluate comparatively their relative content in cryophilous species. The results give:

– 7 cryophilous species out of 67 in mountain forest (10.44%);

– 10 cryophilous species out of 52 in subalpine pine rhododendron forest (19.2%);

– 14 cryophilous species out of 63 in the subalpine and alpine lawns (22%).

Moreover, just cryophilous species alone were found in 25% of samples and were associated to others in 53%. Samples with a rich associated cryophilous fauna are found in alpine lawn and became richer as the altitude increased up to the upper limit of the alpine belt and then to permanently cold habitats.

On the other hand, 11 samples of the alpine lawn had a main species that was cryophilous.

The special case of pine rhododendron forest should be noted. Here the same cryophilous species were found as in lawn but none could be considered as main species. *Anurophorus oredonensis* and *Tetracanthella pyrenaïca* were always found. The presence of these species (some being found in arctic regions) typifies cold, dry and temporary habitats.

Thus, in TCH, as altitude increases, so does the number, the abundance and the association of cryophilous species in the samples.

Comparison of species composition between TCH and PCH

Jaccard's coefficient, with the low value of 0.097, demonstrates the very poor affinity between the two habitats. Among the 18 species common to the two habitats, 7 were cryophilous (*Ceratophysella bidentata*, *Gnathisotoma bicolor*, *Isotomurus* sp., *Proisotoma palustris*, white *Pseudisotoma monochaeta*, black *Pseudisotoma monochaeta*, *Schaefferia emucronata*) while the 11 other common species were able to colonize variable or extreme habitats: *Anurophorus oredonensis*, *Entomobrya nivalis*, *Folsomia quadrioculata*, *Hypogastrura elevata*, *Isotomurus palustris*, *Orchesella* sp., *Protaphorura armata*, gray *Pseudisotoma monochaeta*, mallow *Pseudisotoma monochaeta*, *Pseudosinella suboculata* and *Sminthurinus* sp. Except for two species only found under snow (*Ceratophysella elegans* and *Odontellina nivalis*) the other species in TCH also constitute the main part of the fauna found during the snow-free season in the same habitats (cryophilous species took refuge in permanently cold habitats).

Community structure

1 - Correspondence analysis

A factorial correspondence analysis was computed on the table of TCH samples (92 species versus 121 samples) (*fig.* 8b). A square root transformation conducted of data was made prior to the analysis.

Fourteen factors are needed to account for 50% of the total inertia, with a first factor accounting for only 5.65%. Thus, no single predominant factor seemed to affect the organization of species. Samples and species tend to cluster around the origin, except for a few points at extreme positions providing the most relevant information.

The first factor seems to rank the samples along a gradient going from the temporary cold (level and duration of the snow cover) to samples of increasing cold length due to their orientation and altitude. The most extreme samples belonged to the upper alpine belt, linked to neves and cold water. The first factor thus reveals a gradient of growing duration of cold

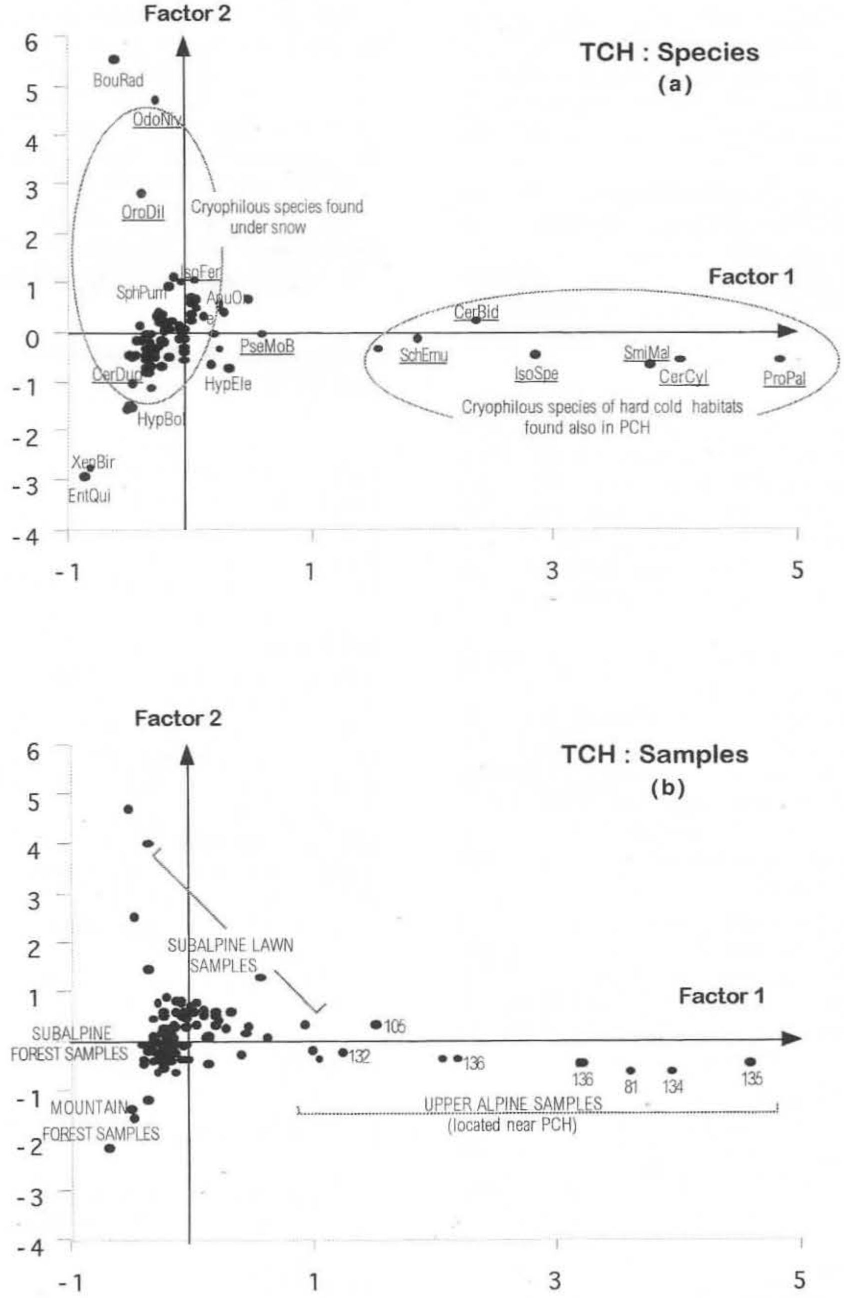


Figure 8. – Results of Factorial Correspondence Analysis of TCH in the F1-F2 plane. Species are plotted in (a), samples are plotted in (b). Both graphs are identically scaled. *See* text for explanations.

together with an attenuation of seasonal fluctuations. It also seems to integrate an additional component linked to the water content of the soil: on one side of the factor, most dry samples were found gradually passing to increasingly humid conditions (running water, sources, thaw water). In fact, these two gradients widely overlap and are without doubt linked to other such that the ordination of the samples is not perfect.

The ordination of the species (*fig.* 8 a) on the first factor confirms the interpretation of the ordination of the samples. The cryophilous species situated at the lowest values of the factor met only in habitats where the cold was the most temporary (*Odontellina nivalis, Orogastrura dilatata, Pseudanurophorus binoculatus* etc.) while the cryophilous species situated at higher values of the factor only met in permanently cold and saturated habitats (*Ceratophysella bidentata,* *Ceratophysella cylindrica*, *Schaefferia emucronata*, *Isotomurus* sp., *Proisotoma palustris*). The most conspicuous example is provided by the situation at the extremity of this factor, of a cryophilous and hygrophilous species, *Proisotoma palustris*, of the alpine belt and the high alpine belt. Several dry species are situated at the other extremity (*Bourletiella radula*, *Xenylla biroi*, *Xenylla brevicauda*).

To test the interpretation of the first axis, a second CFA was computed on the TCH + PCH table (98 species versus 134 samples) after a square-root transformation (*figs.* 9 a and b).

The integration of the new data does not change the general appearance of the graph because all the PCH samples were situated near the highest values of the first axis, like the alpine belt TCH samples, where the most permanent cold prevailed, but far from the center of gravity where the majority of the TCH samples were situated (*fig.* 9 b). The interpretation of the first factor allows anticipation of the position of the

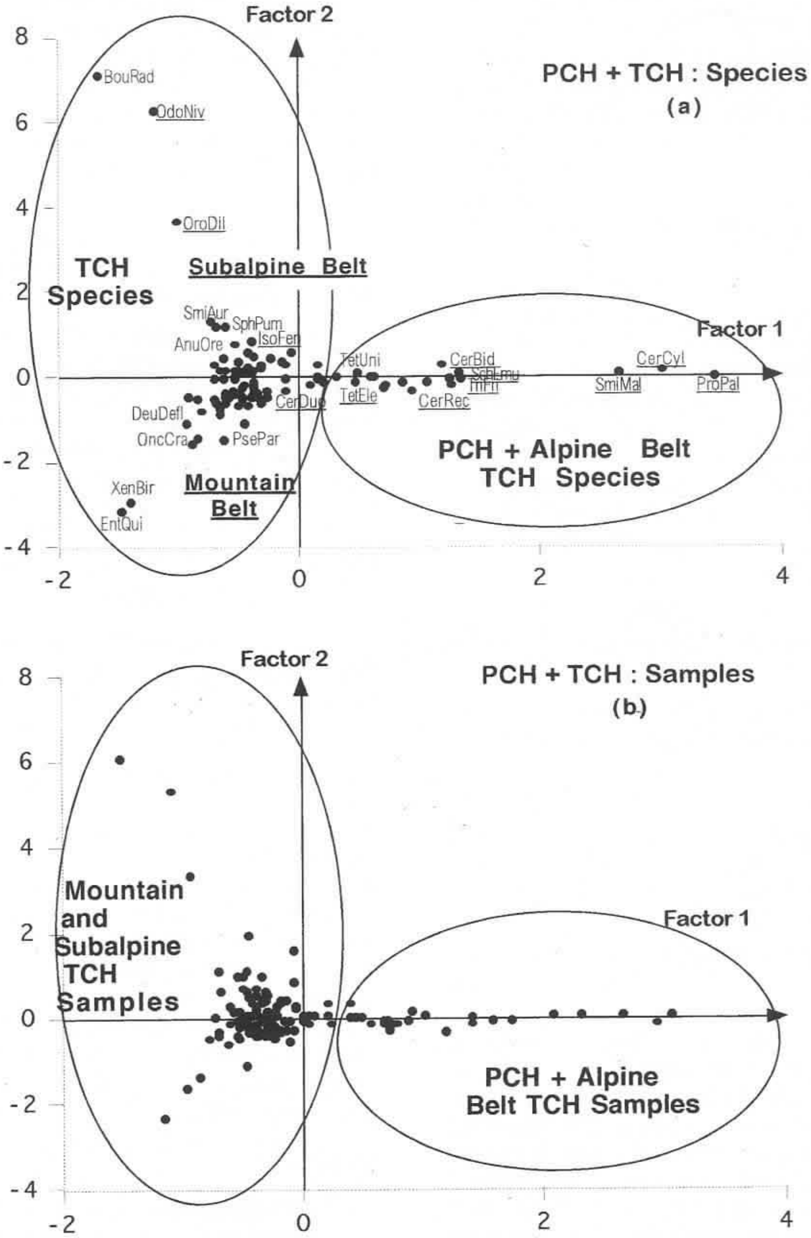


Figure 9. – Results of Factorial Correspondence Analysis of TCH + PCH in the F1-F2 plane. Species are plotted in (a), samples are plotted in (b). Both graphs are identically scaled. *See* text for explanations.

PCH samples to the places where they are effectively situated. The same analysis was performed for the species. All PCH cryophilous species were situated near the highest values (*fig.* 9 a) and near alpine belt TCH species.

The interest of the first factor therefore lies, less in the fact that it provides a possible interpretation of the ordination of both samples and species, than in the fact that it provides a good objective discrimination between the two kinds of habitats under study.

Interpreting the significance of the second factor (4.93% of inertia) is less obvious. It could reveal a complex of factors itself on a gradient going from sheltered habitats up to open habitats. It seems to gather on one of the factors (the strictly sheltered forest habitats) and on the other side increasingly open habitats: those of the rhododendron heath first and then those of subalpine and alpine lawns. The ordination along this gradient is far from perfect because it does not only integrate a gradient of plant formations linked to altitude (like rarefaction of the forest cover) but also other kinds of habitats in lawn (boulders, screes, tufts etc.).

Nevertheless, the first two factors of CFA allow a clear separation of samples along two gradients, with the samples and species of the mountain forest of TCH on the one side and the samples and species of the subalpine and alpine lawns of TCH and PCH on the other side. The samples and species of the subalpine forest (pine rhododendron forest) lie in an intermediate position. Together, the first two factors essentially to seem integrate the "altitude" component which is, in mountain habitats, the key factor of distribution and abundance of species.

CONCLUSION

The structure of Collembola communities in TCH and in PCH exhibit certain well-defined characteristics.

1 - TCH presented a larger species richness (found = 92, estimated = 102) compared to that found by Cassagnau (1961) during the snow-free season. In contrast, PCH exhibited a low specific richness (found = 25, estimated = 30).

2 - TCH exhibits a lower richness in cryophilous species (18% of the all species). They were found in only 53% ofthe samples. On the other hand, PCH presented more cryophilous species (44% of the all species). They were found in 100% of the samples and they were abundant and dominant in a large proportion of samples. Cryophilous species were both more abundant and frequent in PCH than in TCH and although 7 cryophilous species were found common to both TCH and PCH, they were more abundant and frequent in PCH than in TCH (*Ceratophysella bidentata*, *Gnathisotoma bicolor*, *Isotomurus* sp., *Proisotoma palustris*, white *Pseudisotoma monochaeta*, black *Pseudisotoma monochaeta*, *Schaefferia emucronata*). Cryophilous species unique to TCH were associated to snow cover and disappeared after thaw or sought refuge in other isolated habitats. Cryophilous species were regularly found in these habitats and appear to be specialist species (*Ceratophysella recta*, *Hypogastrura estaranhensis*, *Tetracanthella elevata*, *Triacanthella frigida*).

3 - TCH and PCH mainly presented non-specialized fauna dominated by generalistic species like *Pseudisotoma monochaeta*. This species was abundant in the Neouvielle range and particularly in the communities of extreme habitats where it became the major component. Given these results, and with the help of additional studies, it will probably be possible to explain the ecological status of the chromatic variants of this species. Present evidence suggests that the white and black forms appear are cryophilous while the mauve and gray forms appear to be generalistic.

TCH Collembola fauna remains largely stable all over the year even under snow cover (Cassagnau, 1961) but large differences were found in the size and the age-structure of the populations.

4 - In TCH, large β diversity and low evenness (such as high species richness) are in accordance with the heterogeneity of sampled habitats: great range in altitude, plant formations, climatic variations in an apparently homogeneus cold environment. But it should be kept in mind that such values could be affected by artefacts introduced by the time of sampling. Since samples were collected at the end of the snowy period, the populations were likely to be in contrasted stages some begining their development while some were still in their winter stages. In contrast, in PCH, low β diversity and large evenness (such as low species richness) are in accordance with the homogeneity of the samples and, probably their climacic character.

5 - In TCH, the Collembola assemblage is loosely structured probably because it depends upon a large number of factors among which none appears to be predominant. However, it seems possible to identify the interplay of two gradients. The first ranks both samples and species according to the duration of cold. The second ranks both samples and species from sheltered to open habitats. The two gradients are evidently correlated with altitude. TCH and PCH community structures appear to be largely contrasted, some samples become split into two groups following factor analysis. The validity of this distribution is confirmed by the differences found in species richness, β diversity and the value of Jaccard's coefficient (0.097).

The Collembola fauna of Pyrenean cold habitats is representative of the large adaptation potentialities of Collembola to cold-hardiness conditions (review in Leather *et al.*, 1993). Therefore, TCH fauna differs greatly from PCH fauna in as far as cryophilous species composition, species richness and diversity index are concerned. Moroever, correspondence analysis exhibits species and samples ordination along cold-hardiness gradient. Most Collembola species found during the snow-free season (Cassagnau, 1961; Salem, 1973) remain during the snowy season, and become cold-resistant, but cryophilous species are specially characteristic of permanently cold habitats.

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